

Attachment D. Summary of responses to the initial questionnaire. This summary was submitted to three USFWS biologists and two NBS biologists for review, October 1994.

Modeling the Vertical Distribution Of Mussels Inhabiting Riverine Gravel Bars

The goals of this exercise are (1) To describe habitat-use by unionid mussels inhabiting riverine gravel bars, in terms of the depth into the substrate that mussels typically burrow, and including differences among size- or age-classes, species, or reproductive stages, as possible, and (2) To estimate mortality rates for gravel bar mussels that become dislodged from the substrate.

The following estimates were derived from a questionnaire submitted to biologists having expertise in life history and ecology of unionids. Eight biologists responded to the survey; of these, six respondents provided some estimates of vertical distributions and two estimated mortality rates for displaced mussels. *All respondents stressed the paucity of empirical data available for estimating either vertical distribution or mortality rates, and emphasized the need for field research on these basic questions.* In fact, lack of sufficient data certainly contributed to the low overall response to the questionnaire (8 respondents out of 21 biologists who verbally agreed to participate in this exercise).

Most of those responding stated that mussel species and size-classes probably differ in their vertical distributions within a gravel bar matrix, but that available data are insufficient for describing these differences. Most respondents did estimate the overall total depth in the gravel to which a typical assemblage of mussels would occur (i.e., whole animals or the posterior portions of large individuals), and there were a few estimates for size-classes or groups of species. These responses provided the basis for the following general descriptions of vertical distribution (and mortality rates for mussels dislodged from a gravel substrate):

<u>Species</u>	<u>Length-class</u>	<u>Vertical distribution within the substrate</u>	<u>Mortality probability following dislodgment</u>
Juveniles of all spp	0-2 cm	0 - 8 cm deep	0.65
<i>Truncilla truncata</i>	2-5 cm	0 - 10 cm deep	0.3
<i>T. donaciformis</i>	" "	" "	"

<i>Species</i>	<i>Length-class</i>	<i>Vertical distribution within the substrate</i>	<i>Mortality probability following dislodgment</i>
<i>Toxolasma parvus</i>	2-5 cm	0 - 10 cm deep	0.3
<i>Tritogonia verrucosa</i>	" "	" "	"
<i>Quadrula cylindrica</i>	" "	" "	"
<i>Lasmigona complanata</i>	> 2 cm	8 - 20 cm deep	0.3
<i>Q. metanerva</i>	" "	" "	"
<i>Q. nodulata</i>	" "	" "	"
<i>Lampsilis</i> spp.	" "	" "	"
<i>Potamilus alatus</i>	" "	" "	"
<i>Obliquaria reflexa</i>	" "	" "	"
<i>Megalonias nervosa</i>	> 12 cm	0 - 20 cm deep	0.9
<i>Elliptio crassidens</i>	> 10 cm	0 - 20 cm deep	0.9
<i>Amblesma plicata</i>	> 10 cm	0 - 20 cm deep	0.7
All other spp*	>2 cm	0 - 20 cm deep	0.3

\* (and larger *T. verrucosa* and *Q. cylindrica* : see appended page for species list)

Several respondents to the questionnaire raised other critical issues:

- How deeply mussels are buried likely depends on the degree to which the gravel substrate is compacted; mussels are likely to be more shallowly buried in more firmly compacted gravel bars.
- Mussel distributions within the substrate may vary among seasons. Of particular importance, mussels may migrate upward in the substrate to spawn. Spawning individuals may extend above the surface of substrate, and gravid females may occur wholly on top of the substrate. Furthermore, disturbances such as turbulent velocity surges may cause females to abort glochidia.
- Mussels may experience greater difficulty reburying at lower water temperatures.

#### Questions for reviewers:

- (1). Is the above description of vertical distributions reasonable? If not, what changes would you suggest?
- (2). Are the estimates of mortality rates reasonable, or would you suggest changes?
- (3). Can you suggest modifications to these values that would reflect the additional issues noted above? Are there other factors affecting burrowing behavior of mussels in gravel bars that should be considered?

Attachment: Species Under Consideration

The following native unionid mussel species may occur in gravel-bar beds of the Ohio River (approx. River Miles 939 - 981):

<i>Lasmigona complanata</i> (Barnes, 1823)	White heelsplitter
<i>Megaloniais nervosa</i> (Rafinesque, 1820)	Washboard
<i>Tritogonia verrucosa</i> (Rafinesque, 1820)	Buckhorn
<i>Quadrula quadrula</i> (Rafinesque, 1820)	Mapleleaf
<i>Quadrula cylindrica</i> (Say, 1817)	Rabbitsfoot
<i>Quadrula metanevra</i> (Rafinesque, 1820)	Monkeyface
<i>Quadrula nodulata</i> (Rafinesque, 1820)	Wartyback
<i>Quadrula p. pustulosa</i> (Lea, 1831)	Pimpleback
<i>Amblema p. plicata</i> (Say, 1817)	Threeridge
<i>Fusconaia ebena</i> (Lea, 1831)	Ebonysell
<i>Fusconaia flava</i> (Rafinesque, 1820)	Pigtoe
<i>Pleurobema cordatum</i> (Rafinesque, 1820)	Ohio pigtoe
<i>Cycloniais tuberculata</i> (Rafinesque, 1820)	Purple wartyback
<i>Plethobasus cooperianus</i> (Lea, 1834)	Orange-foot pimpleback
<i>Plethobasus cyphus</i> (Rafinesque, 1820)	Bullhead
<i>Elliptio c. crassidens</i> (Lamarck, 1819)	Elephant-ear
<i>Obliquaria reflexa</i> Rafinesque, 1820	Threehorn wartyback
<i>Ellipsaria lineolata</i> (Rafinesque, 1820)	Butterfly
<i>Obovaria olivaria</i> (Rafinesque, 1820)	Hickorynut
<i>Truncilla truncata</i> Rafinesque, 1820	Deertoe
<i>Truncilla donaciformis</i> (Lea, 1828)	Fawnsfoot
<i>Toxolasma parvus</i> (Barnes, 1823)	Lilliput
<i>Leptodea fragilis</i> (Rafinesque, 1820)	Fragile papershell
<i>Potamilus alatus</i> (Say, 1817)	Pink heelsplitter
<i>Ligumia recta</i> (Lamarck, 1819)	Black sandshell
<i>Lampsilis teres f.teres</i> (Rafinesque, 1820)	Slough sandshell
<i>Lampsilis teres f.anodontoides</i> (Lea, 1831)	Yellow sandshell
<i>Lampsilis ovata</i> (Say, 1817)	Pocketbook

# GRAVEL BAR MUSSEL COMMUNITIES: A COMMUNITY MODEL

by

Andrew C. Miller, Barry S. Payne,  
Teresa J. Naimo

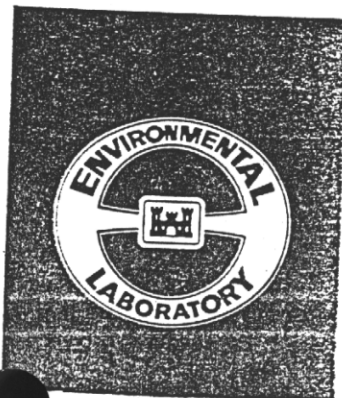
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19. ABSTRACT (Continue on reverse if necessary and identify by block number)  Literature and field data were synthesized to prepare a community model for thick-shelled unionid mussels ( <i>Quadrula</i> , <i>Amblema</i> , <i>Plectomerus</i> , <i>Megaloniaias</i> , <i>Obovaria</i> , and <i>Obliquaria</i> , etc.) that are found in gravel substrate in medium- to large-sized rivers. This model, developed for use with the Habitat Evaluation Procedures of the US Fish and Wildlife Service, can be used for general planning purposes, and to gain a more complete understanding of the biology and ecology of thick-shelled freshwater mussels. The distribution of these species, with respect to the following physical and chemical variables, is reviewed: water velocity, particle type, sediment stability, deposited sediment retained annually, minimum depth, maximum sustained water temperature, minimum sustained dissolved oxygen, and calcium hardness. Physical, chemical, and biological characteristics of large river systems where these organisms are found are reviewed. The biology and			
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19. ABSTRACT (Continued).

ecology of freshwater mussels, including feeding, locomotion, behavior, reproduction, and early development, are discussed.

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## PREFACE

In 1980, the Office of the Chief of Engineers (OCE), US Army, funded a 2-year program on freshwater molluscs at the US Army Engineer Waterways Experiment Station (WES) through the Environmental Impact Research Program (EIRP), Work Unit 32390. Following completion of that work, plans were made to prepare a community model for freshwater mussels (family Unionidae) that live in gravel bars in large rivers. With funds from the US Army Engineer Districts of Louisville, Nashville, and Mobile, as well as EIRP, quantitative data were obtained from mussel beds in large rivers. The model described in this report is based upon those studies.

This report was prepared by Dr. Andrew C. Miller, Dr. Barry S. Payne, and Ms. Teresa J. Naimo of the Aquatic Habitat Group (AHG), Environmental Resources Division (ERD), Environmental Laboratory (EL), WES. Dr. W. D. Russell-Hunter, Syracuse University, Syracuse, N. Y., prepared Part III of this report and assisted in preparation of the Suitability Index curves. The report was edited by Ms. Marsha Gay of the WES Information Products Division, Information Technology Laboratory.

Studies on freshwater molluscs at WES are under the general supervision of Dr. Thomas D. Wright, Chief, AHG; Dr. Conrad J. Kirby, Chief, ERD; and Dr. John Harrison, Chief, EL. Dr. Roger T. Saucier is WES Program Manager of EIRP. The Technical Monitors for the EIRP are Dr. John Bushman and Mr. Earl Eiker, OCE, and Mr. Dave Mathis, Water Resources Support Center.

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CONVERSION FACTORS, NON-SI TO SI (METRIC)  
UNITS OF MEASUREMENT

Non-SI units of measurement used in this report can be converted to  
SI (metric) units as follows:

<u>Multiply</u>	<u>By</u>	<u>To Obtain</u>
atmospheres (standard)	101.325	kilopascals
cubic feet	0.02831685	cubic metres
cubic yards	0.7645549	cubic metres
feet	0.3048	metres
miles (US statute)	1.609347	kilometres
tons (2,000 pounds, mass)	907.1847	kilograms

## GRAVEL BAR MUSSEL COMMUNITIES: A COMMUNITY MODEL

### PART I: INTRODUCTION

#### Background on Mussels

1. Freshwater mussels are a unique resource with economic, cultural, and ecological value. In this country their meat has been used for food, and the shells used to make ornaments, tools, and pearl buttons. Presently, shells are collected and shipped to the Orient where they are processed into inserts for the cultured pearl industry. Because they are long lived and practically nonmotile, their presence at a site provides evidence of previous habitat conditions. There are over 200 species of freshwater mussels in this country; of these, 28 are on the list of Endangered Species and are protected by the Endangered Species Act.

2. Freshwater mussels can be collected in ponds, lakes, streams, and large rivers. When present, they often dominate the benthic fauna, both in numbers and biomass. They can be found in a variety of substrates including mud, silt, sand, and gravel, or between and under large rocks. However, they are most likely to be found in a mixture of sand, gravel, and mud in large rivers of the central United States. A gravel bar habitat can support from 15 to more than 25 species; densities can exceed 100 per square metre.

#### Habitat-Based Evaluation Methods

3. In the 1970s the US Fish and Wildlife Service began development of the Habitat Evaluation Procedures (HEP) for use in impact assessment and habitat management. The HEP is an accounting system that enables a user to rate the value of habitat for organisms of interest. Central to the HEP are Suitability Index (SI) curves, which quantify the response of an organism to physical variables such as depth, substrate type, or water velocity. These SI curves can be grouped into a Habitat Suitability Index (HSI) model. HSI models have been prepared for a variety of birds, mammals, fishes, and selected invertebrates and are available from the US Fish and Wildlife



Service. An HSI model is a complex hypothesis of species-habitat relationships and is not a statement of proven cause and effect."

4. The HSI model described herein deals with mussel species that inhabit gravel bars in large rivers. Literature and field data pertaining to these mussels have been synthesized into a 0.0 to 1.0 index score that quantifies the ability of habitat to provide necessary life requisites for these organisms. Assumptions used to transform habitat use information into the index scores are noted, and guidelines for application of the model are described.

#### Purpose and Scope

5. The purpose of this report is to describe an HSI model for thick-shelled freshwater mussels that can be used for impact analysis, planning, and resource management conducted by Federal, state, and private agencies. This model is intended primarily for mussels in the following genera: *Quadrula*, *Amblema*, *Plectomerus*, *Megalonaias*, *Obliquaria*, and *Obovaria*.

## PART II: CHARACTERISTICS OF LARGE RIVER HABITATS

### Hydrology

6. Although there are over 3.25 million miles\* of streams in the 48 contiguous states, large rivers dominate the landscape (Figure 1). Flowing water or lotic systems are characterized by unstable bottoms, high turbidity, high dissolved oxygen, meandering channels, and unidirectional, occasionally turbulent flow. Of the 76 cm of rainfall received by this country annually, approximately 23 cm contribute to the flow of rivers (Figure 2).

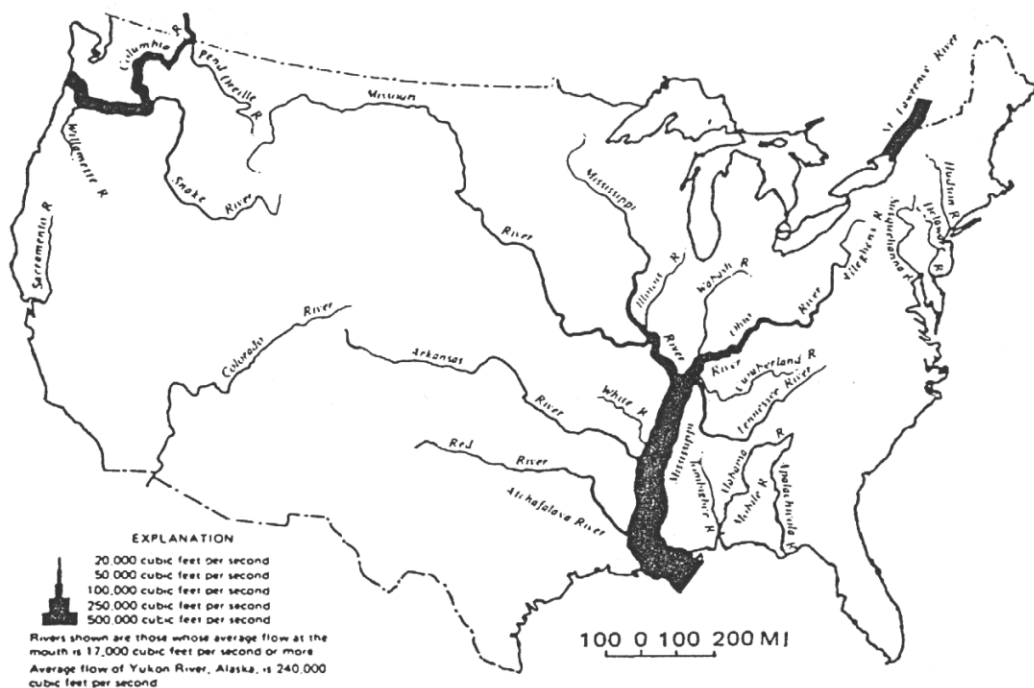


Figure 1. Major rivers in the United States based on discharge (from Geraghty et al. 1973)

7. Lotic systems can be categorized based upon the following three factors: flow, drainage pattern, and order. Flow can be ephemeral and occur after storms, or intermittent and exist only during the wet season. Most streams are perennial and persist throughout the year. Drainage pattern is dependent upon geomorphology: dendritic types are in flatlands, rectangular types are typical of faulted areas, and trellis types are found where there is

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\* A table of factors for converting non-SI to SI (metric) units of measurement is found on page 4.

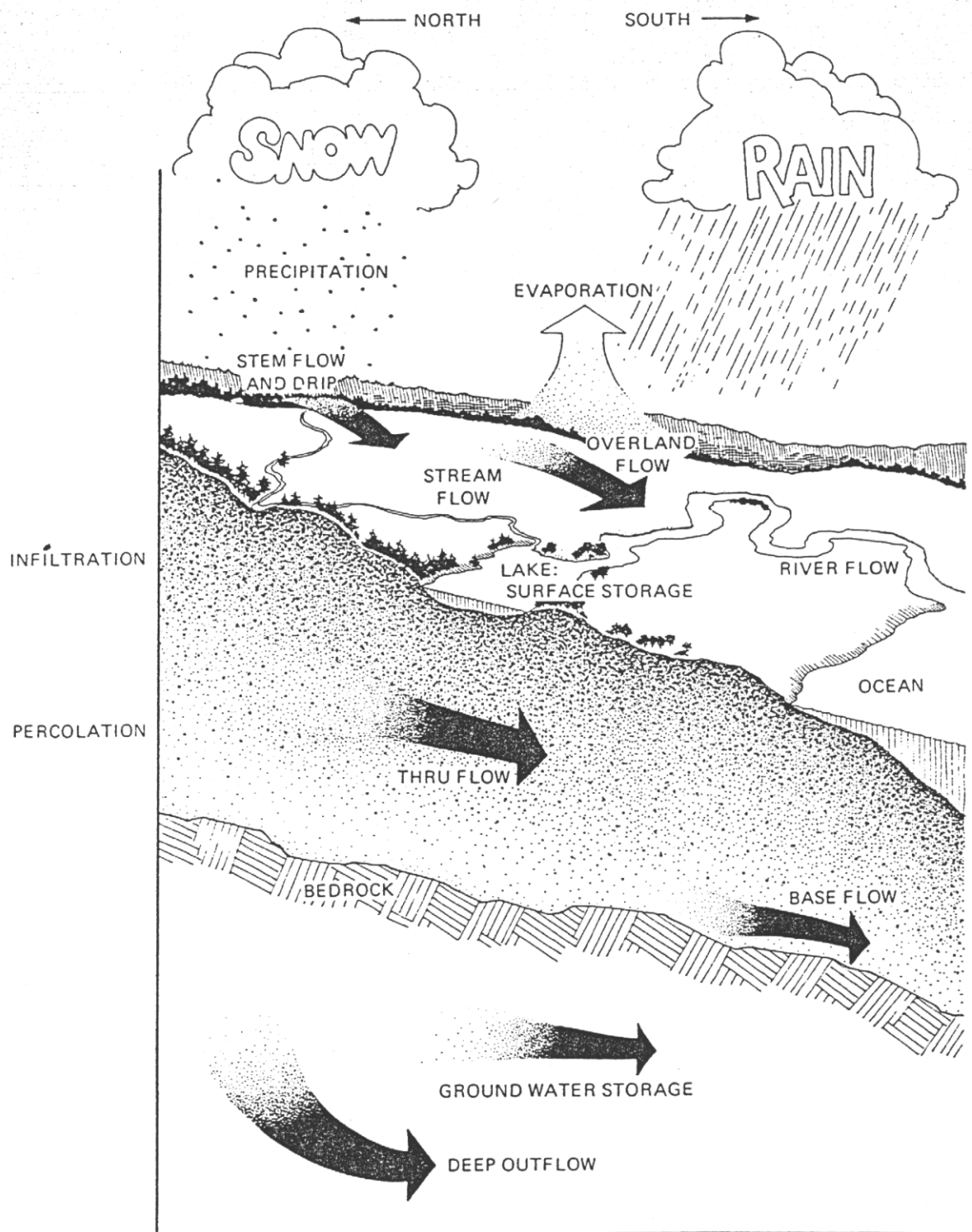


Figure 2. Hydrologic processes in rivers

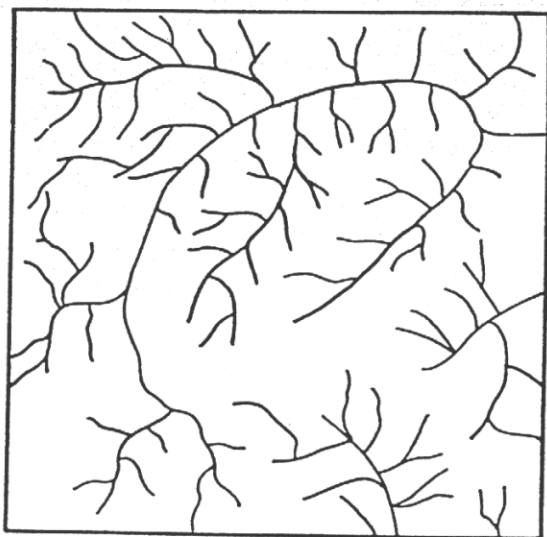
folding of the strata (Figure 3). A stream ordering system was devised by Horton in 1945 as a means to differentiate waterways (Figure 4). A headwater stream has an order of 1; when two first-order systems join, they produce a second-order system. Order increases moving from headwaters to mouth; the highest river order is 12. Each order has its own unique physical and biological characteristics. Of the 3.25 million miles of flowing water, 85 percent are first- and second-order streams. The lower Mississippi, Missouri, and Ohio Rivers are 12th-, 8th-, and 7th-order systems, respectively.

8. Velocity, an important hydrologic parameter, influences erosion rates, sediment transport, and distribution of aquatic organisms. In rivers velocities can range from near zero to more than 9 m/sec (Coker et al. 1921). In rivers with velocities greater than 30 cm/sec, aquatic insects, worms, and most other invertebrates seek shelter among rocks and other obstacles. In the boundary layer (1 to 3 mm) along the stream bottom where the current approaches zero (Figure 5), attached algae, immature insects, and mussels can exist because they are protected from high-velocity water. In large rivers, high water velocity can limit the presence of bivalves. In the midchannel of certain rivers, velocities exceed 60 cm/sec; such habitats are inimical to unionids.

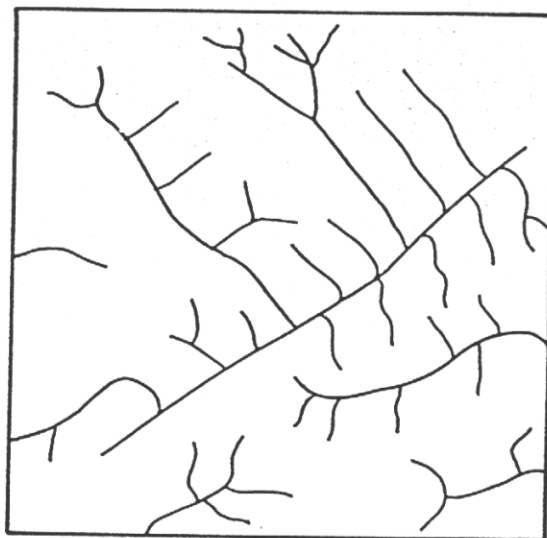
9. Rivers have the ability to transport large quantities of material (or suspended load) in the water column (Reid and Wood 1976). The Mississippi River at Vicksburg carries approximately 1 million cu yd per day (Mathis et al. 1981). Livingstone (1963) calculated that the rivers of the world deliver 3.9 billion tons of dissolved material to the oceans annually. Although 10 constituents accounted for the majority of the dissolved material, calcium, bicarbonate, silicate, and sulfate predominated. Small streams are a source of particulate and dissolved organic material for the larger rivers. Leaves, twigs, and other vegetation are processed in small streams and exported downriver.

#### Erosion and Deposition

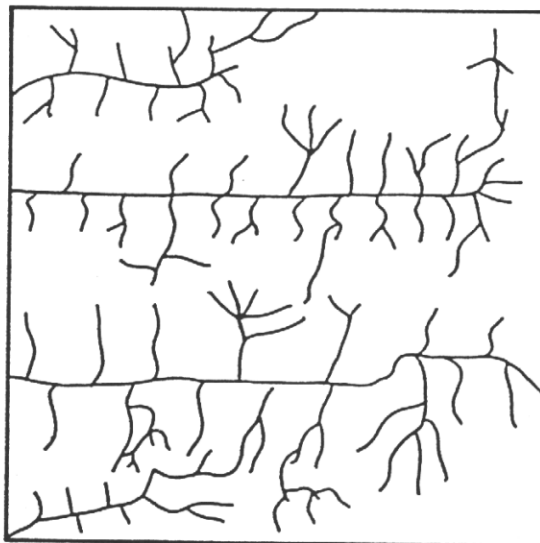
10. High velocity and maximum erosion in a river take place next to concave banks on the outside of bendways (Figure 6). In a straight reach the



a. Dendritic



b. Rectangular



c. Trellis

Figure 3. Common drainage patterns  
in flowing water systems

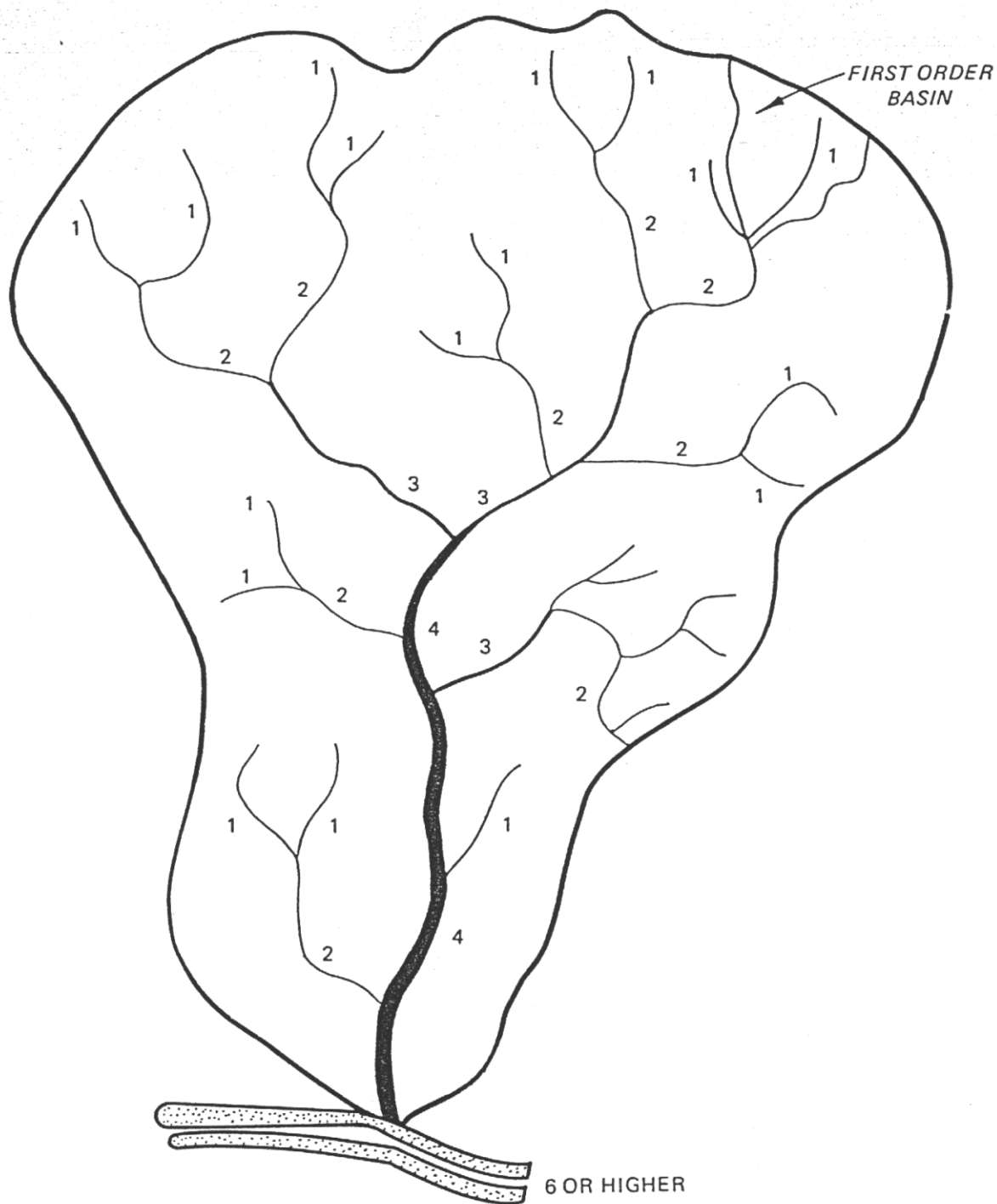


Figure 4. The stream ordering system

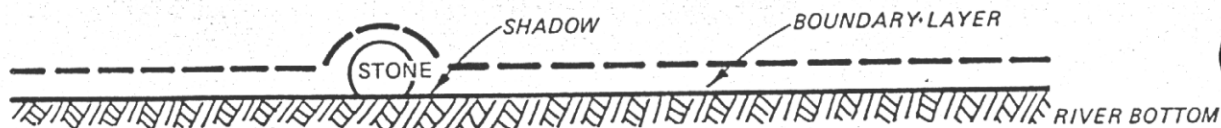


Figure 5. The boundary layer in rivers

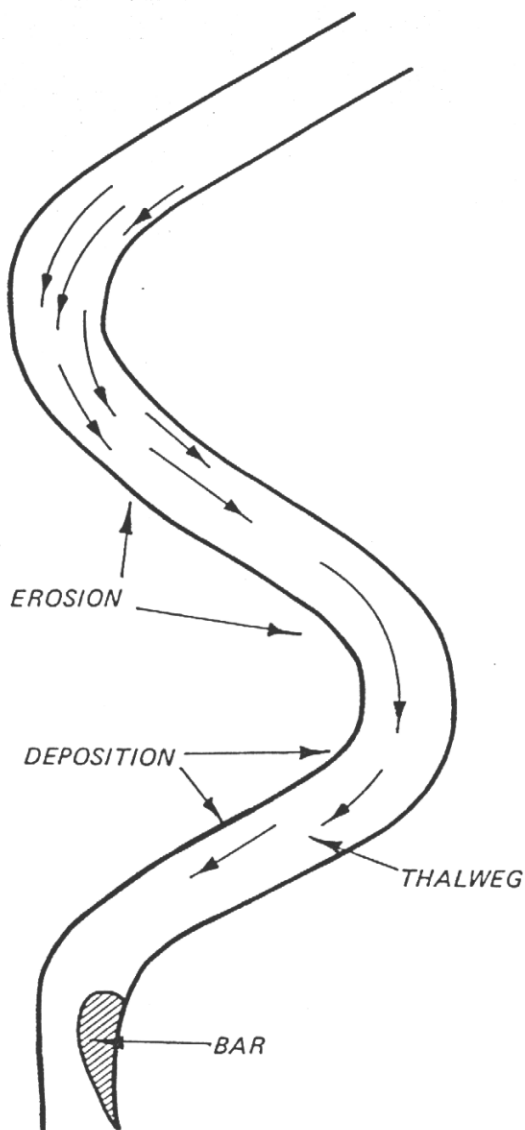
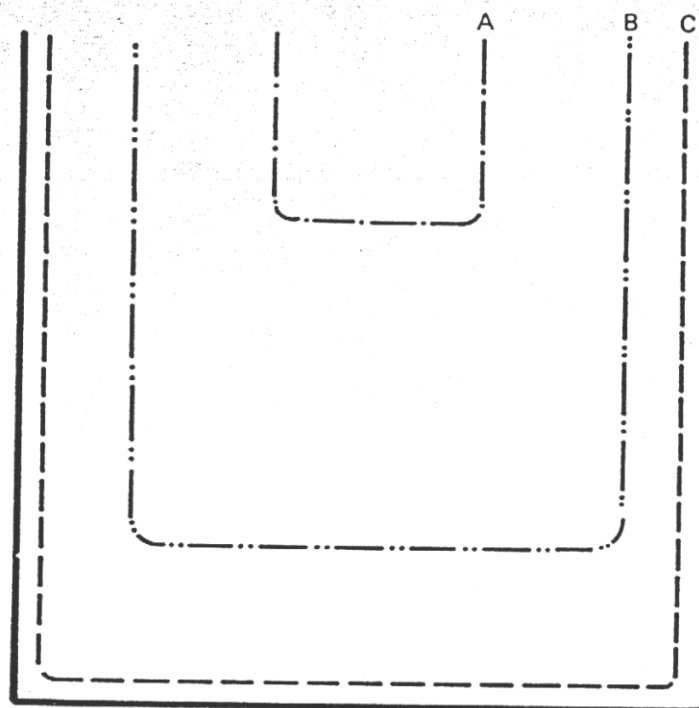


Figure 6. Idealized flow pattern of a large river (modified from Leopold et al. 1984)

maximum velocity is often near the center (thalweg) and at approximately one-third the depth (Figure 7). An erosional zone or riffle is found where the substrate is scoured and the currents are usually greater than 30 cm/sec. Depositional zones, or pools, occur where currents are reduced and fine particles accumulate. A spate is a short period of high water caused by a





A = MAXIMUM FLOW AT 1/3 DEPTH AND CENTRALIZED  
 B = MEAN VELOCITY AT 6/10 DEPTH  
 C = MINIMUM FLOW AT RIVER EDGES

Figure 7. Velocity differences in stream cross section

storm, which frequently erodes and reworks base material. After a flood, the river will return to base flow although the time required depends on stream size and intensity of the event.

11. In large river habitats, molluscs exist in both depositional and erosional zones. In the St. Francis River, northern Arkansas, large numbers of *Proptera capax* can be collected in depositional, straight reaches of the river. The mussel beds in the Tombigbee, Ohio, Cumberland, and Upper Mississippi rivers are in erosional zones. At these sites, however, current velocities are usually less than 30 cm/sec and the substrate is stable. Coker et al. (1921) discussed the cross-sectional distribution of mussels in a river. It was determined that the nature of the substrate (i.e. erosional or depositional), rather than the water depth, was most the important in determining the location of bivalves. Because bivalves live partially buried in the substrate, they avoid the erosive action of high-velocity, sediment-laden

water. When molluscs are found in high-velocity sites, their shells can be heavily eroded.

### Substrate

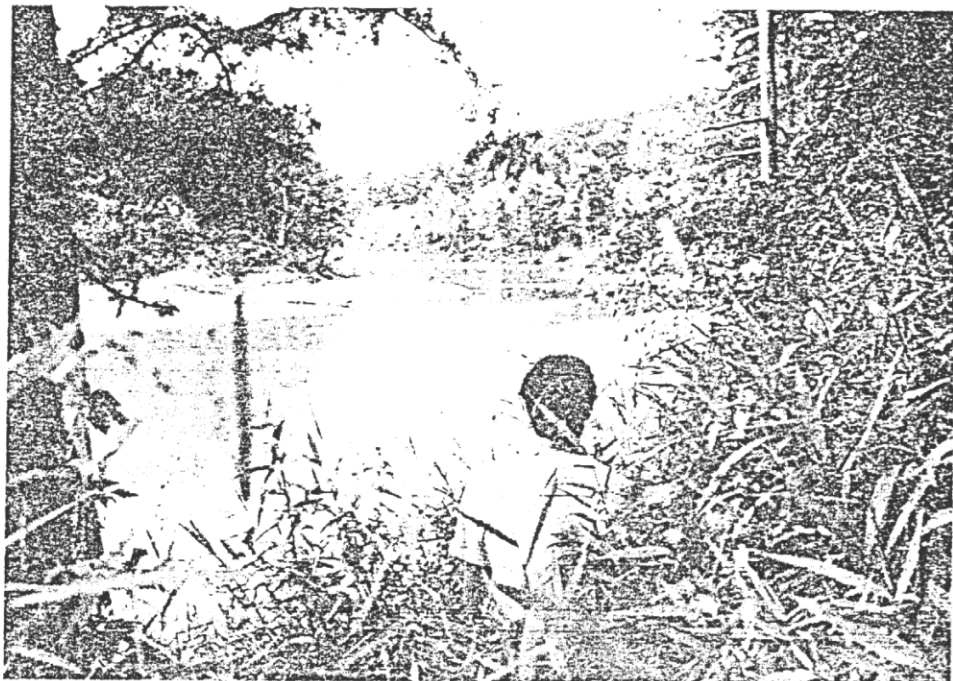
12. Substrate conditions depend on the nature of the surrounding terrain and on the size of the river (Reid and Wood 1976). In the lower reach of a river, the substrate is usually characterized by silt, mud, and detritus (Table 1). In the middle reaches, coarser materials are found, while in the upper reaches, large rocks and boulders predominate. In most rivers, mean particle size decreases in a downstream direction, and a correlation exists between particle size and slope (Hawkes 1975, Hynes 1970). Stream orders 1-3 have large-sized coarse materials, and orders 4-6 exhibit both coarse and fine materials. Fine materials predominate in orders greater than 7. Gravel bars in rivers are depositional sites that occur when velocity declines and coarse materials drop out of the water column (Figure 8). These habitats provide permanent, stable substrate for mussels.

Table 1  
Major Differences Between Headwater and Large River Systems

<u>Parameter</u>	<u>Headwater Streams</u>	<u>Large Rivers</u>
Substratum	gravel rock	sand mud clay silt
Turbidity	low	high
Light penetration	moderate	low
Major invertebrate functional group	shredders, scrapers, and predators	collectors
Total dissolved solids	low	high
Canopy cover	high	low
Gradient	high	low
Suspended particulates	low	high
Dominant fish group	trout sculpin stonerollers	drum buffalo catfish



a. Natural gravel bar in the Tombigbee River near Aliceville, Ala.



b. Artificially placed gravel bar habitat in an abandoned channel of the Tombigbee River near Columbus, Miss.

Figure 8. Gravel bar habitats in flowing water systems.

## Macroinvertebrates

13. Macroinvertebrates comprise four functional trophic groups: scrapers, shredders, collectors, and predators (Table 2, Figure 9). Scrapers are organisms such as snails, caddisflies, and other herbivores that feed on attached algae and associated bacteria and detritus. Shredders feed on wood, as well as decomposing and living plant material. Certain species of mayflies, caddisflies, blackflies, and all species of freshwater mussels are collectors which feed on fine particulate organic matter that has been recently deposited or is suspended in the water column. Predators, which either engulf or pierce their prey, range in size from small midges (less than 1 cm), to dragonflies, damselflies, dobsonflies, and fishes (Merritt and Cummins 1984).

14. The proportion of each functional group in a lotic system varies with stream order. In rivers greater than seventh order (Mississippi, Amazon, or Nile), the community usually consists of 90 percent collectors and 10 percent predators. Suspended particulate organic matter less than 1.0 mm such as bacteria and detritus is a large component of the available food source. Bivalves, including the unionids, as well as the Asian clam, *Corbicula fluminea*, can achieve their greatest abundance in these habitats.

15. Erosional zones of rapidly flowing waters, where all but the coarse substrate has washed away, have stone flies, mayflies, blackflies, and caddisflies adapted for attachment and clinging or avoiding current (Moon 1939). Invertebrates common in high-velocity water include true flies such as Blepharoceridae, Simuliidae, and Deuterophlebiidae and many species of stoneflies and mayflies. In headwater streams animals such as shredders and grazers obtain their food from the bottom or along shoreline areas (Cummins 1974, Cummins 1975, Vannote et al. 1980, and Minshall et al. 1983).

16. In some situations, trophic conditions (presence of suitable food) can be as important in explaining distribution of unionids as physical or chemical factors (Green 1971). Certain species of mussels are found only in small streams (Table 2). In these habitats bivalves are usually not common and are not restricted to large groups or beds as they are in systems greater than third or fourth order. Since mussels are nonmotile and dependent upon organic matter brought to them, they may be limited in upstream reaches where particulate organic matter is scarce.

Table 2  
Major Functional Groups in Aquatic Systems  
(from Merritt and Cummins 1984)

Group	Dominant Food	Representatives	
		Small Rivers	Large Rivers
Scrapers	Periphyton	Coleoptera: <i>Psephenidae</i> Mollusca: Gastropoda	Ephemeroptera <i>Stenonema</i> spp. <i>Heptagenia</i> sp.
Shredders	Wood, decomposing and living plants.	Coleoptera: <i>Lara</i> sp. Diptera: <i>Tipulasp.</i>	Chironomidae <i>Glyptotendipes</i> spp.
Collectors	Decomposing and fine particulate organic matter	Trichoptera: <i>Cyrmellus fraternas</i> Pelecypoda: <i>Ptychobranchus</i> sp.	Trichoptera: Hydropsychidae Pelecypoda <i>Fusconaia ebena</i> <i>Amblema plicata</i> <i>Quadrula</i> sp. <i>Corbicula</i>
Predators	Living animal tissue	Odonata: <i>Calopteryx</i> sp. Megalopectera: <i>Corydalis</i> sp.	Diptera: <i>Chaoborus</i> spp. Odonata: <i>Gomphus</i> spp.

17. Maximum invertebrate diversity (aquatic insects, worms, and crustaceans) usually occurs in the midreaches of fourth- and fifth-order streams. These areas are characterized by large physical diversity, i.e., presence of pools, riffles, and runs, and an abundance of in-stream structure such as cobble, gravel, logs, brush and aquatic vegetation, and large annual temperature fluctuations (Vannote et al. 1980).

#### Fishes

18. For most species of fishes, the substrate characteristics are important mainly during breeding. Dissolved oxygen is not usually limiting in rivers, except for species such as brook trout (*Salvelinus fontinalis*), which survive only in cold water systems. The major problem riverine fishes encounter is maintaining themselves against a constant current. Some fishes

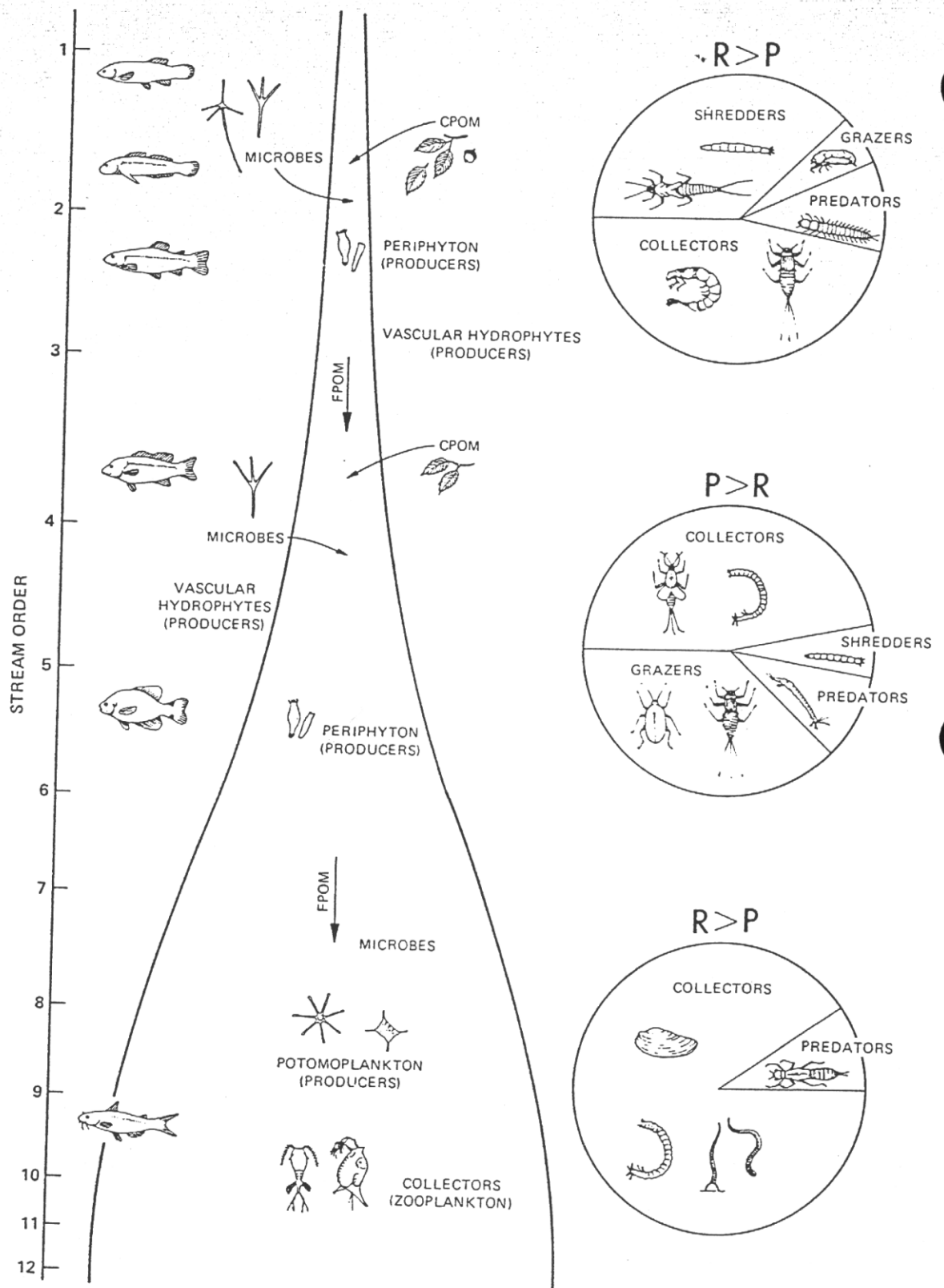


Figure 9. Functional feeding groups in flowing water systems. In many rivers after order 4, freshwater mussels are significant components of the invertebrate community (modified from Cummins 1974).

avoid this by seeking shelter; others inhabit low-velocity areas except while feeding.

19. Fishes common to headwater systems include darters, stone rollers, sculpins, and madtoms, which feed principally on invertebrates which they obtain from gravel or which are associated with brush and other forms of cover. Fishes common to large rivers include plankton feeders such as shad and paddlefish, and predators such as bass, sunfishes, and sauger. Bottom-feeding fish such as drum and catfish are common inhabitants in large rivers and feed on small mussels and *Corbicula*. Large rivers have a greater diversity and density of fishes, hence a greater opportunity for available fish hosts to carry immature stages of freshwater mussels. This is an additional reason for reduced density and diversity of molluscs in headwater streams. (See Part III for discussion of reproduction in bivalves and Appendix A for a list of fish hosts for mussels).

#### Anthropogenic Effects

20. In this country rivers are used as a source of water for domestic and industrial uses, as a repository for wastes, and as means of transporting bulk commodities. Channel maintenance, bank protection, clearing and snagging, and dredging are actions which have been commonplace since the latter part of the 19th century. In addition, the development of rivers such as the Ohio and Mississippi for navigation has led to construction of large, run-of-the-river reservoirs. These reservoirs cause reduced turbidity, longer water retention times, and higher primary productivity than existed prior to commercial navigation. They have been responsible for converting the fauna from those inhabiting shallow, fast-water habitats to those tolerant of lake-like conditions. Certain thick-shelled unionids (belonging to the genus *Dysnomia*) used to be more abundant when riffles and shoals were a significant aspect of large rivers (Stansbery 1971).



### PART III: BIOLOGY OF FRESHWATER BIVALVES

#### Evolution

21. The bivalve clams and mussels of fresh waters are, in all aspects of their anatomy, typical members of the phylum Mollusca and of the class Bivalvia. While this is also true of most aspects of their somatic physiology (including feeding mechanisms, digestion, growth, locomotion, and behavior), they are clearly atypical in their life cycle patterns and nonmarine habitats. The evolutionary background of these contrasting facts is important to an understanding of the ecological constraints upon, and the general habitat distributions for, the few specialized genera of freshwater bivalves.

22. One of the most successful patterns of animal construction is the molluscan plan, which is characterized by a soft, hydraulically moved body contained within a hard calcareous shell. There are more than twice as many species of molluscs as there are of vertebrates, and only the arthropods are clearly a more numerous and more successful group (Russell-Hunter 1979, 1983). There are probably 110,000 living molluscan species, and the biomass of certain of these species can dominate the lower trophic levels of many aquatic ecosystems. In fact, in the global economy of the oceans, certain benthic bivalves are second only to planktonic calanoid copepods in the annual caloric turnover for animal tissues in food chains. Although molluscs are largely marine, there are a few, highly successful nonmarine forms. Certain bivalve genera are very important in the faunas of estuarine and fresh waters, as are the more diverse groups of freshwater gastropods. The only terrestrial molluscs are snails (class Gastropoda).

23. Freshwater bivalve molluscs belong to a limited number of largely cosmopolitan genera classified in three lamellibranch superfamilies (Unionacea, Corbiculacea, and Dreissenacea). Two of these are more important: the Unionacea (the large freshwater mussels) and the Corbiculacea (the small fingernail and pea clams). Throughout the world, the unionacean mussels are generally associated with larger, relatively permanent river systems. In their soft parts most freshwater mussels are structurally rather stereotyped. Unionaceans show adaptive radiation principally in shell shape and shell sculpture with their internal anatomy showing few of the adaptive specializations that give particular interest to functional morphology in most

superfamilies of marine bivalves. Specific anatomical modifications for particular habitats do not usually occur, although four tropical genera in the unionacean family Etheriidae (Yonge 1962) do show structural specialization for life in turbulent waters. River systems in the temperate latitudes of the world are populated by remarkably uniform genera of mussels. In the Northern Hemisphere most genera (including *Anodonta*, *Quadrula*, *Elliptio*, *Lampsilis*, and *Margaritifera*) are cosmopolitan in distribution; and for a few genera, closely similar sets of species are found not only in North America, but also in rivers of appropriate size in Northwest Europe, Central Asia, and Mongolia. Other species are clearly endemic, and even limited to particular river systems.

24. Though basically more uniform in structure, unionacean mussels differ from marine bivalves in having an obligatory parasitic stage in their life cycle, which can be species specific. After the fertilized eggs have been incubated in marsupial embayments of the exhalant gill cavity of the female mussel, they are released as glochidial larvae for a required period, as parasites on a vertebrate host (usually a fish species). After further growth (normally in a mutually formed cyst), juvenile mussels break out to settle on appropriate stable substrates. As in all animals with parasitic stages, reproduction in unionaceans is characterized by remarkably high numerical fecundity. It is important to reemphasize that, apart from this parasitic stage in their life-cycles, all other aspects of structure and function in freshwater unionacean mussels are typical of those found throughout the subclass Lamellibranchia and class Bivalvia.

### Systematic Survey

#### Class bivalvia

25. Forming the most uniform of the three major classes in the phylum Mollusca, there are probably about 31,000 species of bivalves, all with the shell in the form of two calcareous valves united by an elastic hinge ligament. As in all molluscs, the shape of the shell is determined by the growth of the mantle (or pallium), the fleshy fold of tissues which enfolds the visceral mass and which, in the bivalves, has become elongate and laterally compressed so that all parts of the body (visceral mass, muscular foot, and all pallial organs including gills) lie within the mantle cavity and

the head is lost. (Bivalves were formerly referred to as the Mollusca-Acephala.) Obviously, normal cephalic sense organs would not be of much value within the mantle cavity and out of contact with the environment. In all molluscs the middle lobe of the mantle edge also bears sense organs, and in the bivalves these show their fullest development as chemoreceptors, as mechanoreceptors, and even as eyes. (Actually, no freshwater mussel has well-developed eyes like those of marine scallops, but all have light-sensitive patches of tissues in the postero-ventral parts of the mantle edges.)

26. In the bivalves, as in all other molluscs, the mantle and its secreted shell form a single structural entity. The description found in most textbooks of two discrete valves united by a ligament of different origin is totally erroneous. Developmentally, a single mantle rudiment appears early in the larva, and although growth patterns are such that anterior and posterior embayments appear in the originally dome-shaped rudiment, there always remains a mantle isthmus. Usually, the material secreted by a mantle isthmus contains proportionately less crystalline calcium carbonate and proportionately more elastic tanned proteins, and forms the ligament of the bivalve shell. This elasticity is very important to the mechanical functioning of the bivalve.

27. In all bivalves the shell is closed by the action of adductor muscles, which run from one shell to the other. These, the largest muscles in any bivalve, have no single antagonist but can be stretched by several mechanisms, which include the elasticity of the horny hinge ligament and several kinds of hydraulic systems. The relative importance of each method varies in different types of bivalves. For example, in species of *Elliptio* and of *Margaritifera*, movement of blood into the sinuses of the foot and pedal protraction ventrally can force the shell valves apart and thus stretch the adductor muscles to their precontraction length. In contrast, in species of *Anodonta* and of *Strophitus*, the elasticity of the ligament is more important. In these, as in the Corbiculacea, Dreissenacea, and a wide variety of marine bivalves, the elastic ligament connecting the shell valves dorsally is under strain (tensile or compressive, depending on shell hinge structure) when the valves are closed. The force derived from this tends to open the valves. In fact when the adductor muscles of a bivalve contract, closing the shell, they are also doing the work which will subsequently reopen the shell valves. This work involves compression or extension of the "springs" of the ligament.

28. Although the Bivalvia are remarkably uniform in anatomy, there are three distinct subclasses, unequal in extent and in ecological significance. The great majority of living bivalves belong to the major subclass Lamellibranchia, which are characterized by having enormously enlarged gills used in filter feeding. All freshwater bivalves are lamellibranchs. The other two, more minor, groups comprise the subclasses Septibranchia and Protobranchia. The gills are replaced by a muscular septum in the septibranchs, a relatively rare group from moderate ocean depths. The subclass Protobranchia is of greater evolutionary interest, since its genera are in many ways intermediate in form and function between the specialized filter-feeding lamellibranchs and more generalized molluscan stocks.

Subclass lamellibranchia

29. The diagnostic feature for lamellibranchs is their possession of a pair of enormously enlarged and folded gills. Each lamellar gill has many elongated filaments, and although it is homologous both functionally and morphologically with the ctenidium in gastropods (and all other molluscs) in terms of its blood vessels and arrangement of cilia and so on, is far more extensive than is required for the respiratory needs of the animal. It is now the major organ of food collection in these filter feeders. Briefly, a water current through the mantle cavity is created by the lateral cilia. This flows through between the filaments of the ctenidium from the inhalant part of the mantle cavity to the exhalant region. Any particulate matter remains on the inhalant face of the gill, and frontal cilia and mucus are used to make chains or boluses of material to pass to the mouth. The structures and functions involved in this diagnostic feeding mechanism are described more fully in the following paragraph.

30. In many time-honored and popular classifications of the bivalves, the many superfamilies of lamellibranchs were divided between two orders Filibranchia and Eulamellibranchia. The ordinal name Filibranchia was used for those bivalves with ctenidial filaments in their lamellar gills held together by ciliated junctions. In contrast, the superfamilies of the order Eulamellibranchia were defined as having gill filaments united by fused tissues, thus forming a mechanically stronger and more efficient filtering apparatus for feeding. Although attractive on functional grounds, this division is unacceptable phylogenetically since the eulamellibranch condition has been independently evolved in several different stocks of bivalve families. Better

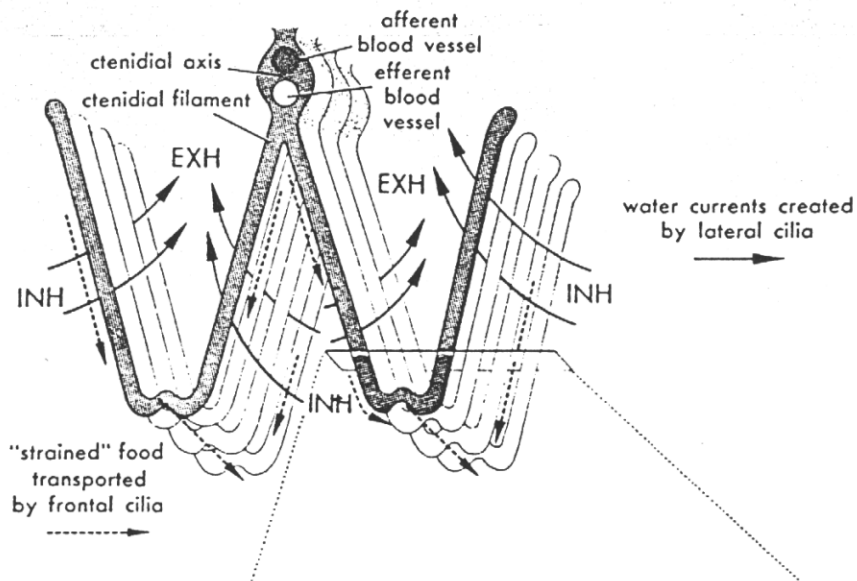
modern classifications do not employ these two ordinal names. Among freshwater forms, the Dreissenacea show the filibranchiate condition, but all the Unionacea are eulamellibranchiate.

#### Superfamily Unionacea

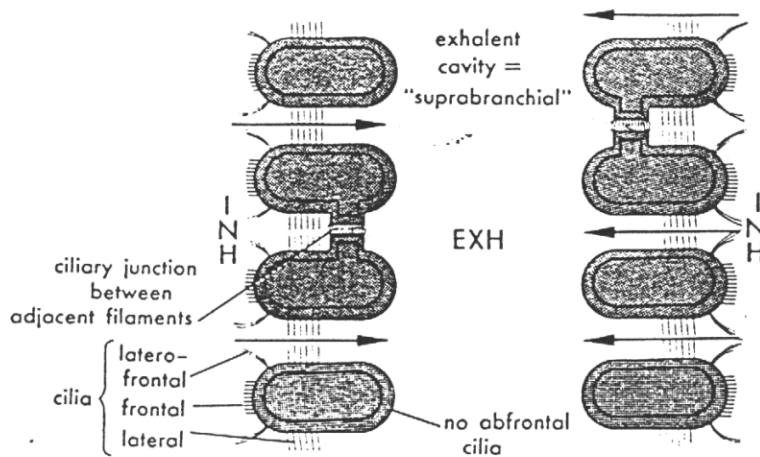
31. There are several alternative ordinal arrangements for the many well-established superfamilies of lamellibranch bivalves. Many neontologists employ a relatively conservative classification which divides the subclass Lamellibranchia into six orders containing living forms, and assigns the superfamily Unionacea to the order Schizodonta. The superfamily or suborder Unionacea (or Unionoidea) comprises freshwater bivalves, dimyarian and relatively symmetrical, mostly with schizodont hinges, with mantle edges almost completely unfused, with a large plough-shaped foot, and with the two large ctenidia in four relatively posterior demibranchs which can be used as marsupia in brooding larvae. Recent authorities (including Burch 1973) place the unionaceans of North America in three families, separating both the Margaritiferidae and the Amblemidae from the large worldwide family Unionidae, but there remains some resistance to these separations. Elsewhere within the superfamily, the family Mutelidae is largely limited to the Southern Hemisphere, and the family Etheriidae includes the peculiar oysterlike forms from turbulent rivers in the tropics. The cosmopolitan family Unionidae comprises a very large number of species and subgenera, although it should be noted that, in many classifications of freshwater mussels, "splitting" at the generic and subfamilial levels is probably excessive. Compared with the characters used in the generic systematics of most families of marine bivalves, those used in the Unionidae are relatively trivial.

#### Filter-Feeding Mechanism

32. The majority of bivalves (perhaps 29,000 out of 31,000 living species including all Unioniacea) have essentially the same feeding process. The following description would apply to any of them, although Figure 10 is largely based on the structures in mussels such as *Mytilus*. In all lamellibranchs, the lateral cilia produce the water current between adjacent filaments. This water passes ventrally into the inhalant part of the mantle cavity, and thence through the gills to the exhalant chamber above and within them. All food organisms and all suspended material are accumulated on the



a. Stereogram of folded filaments in ctenidium



b. Horizontal section through a demibranch (a half ctenidium)

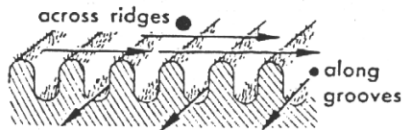
Figure 10. Archetypical gill structure in lamellibranchs (from Russell-Hunter 1979)

inhalant faces of the gill lamellae. Such material and food are then moved by the frontal cilia toward the ventral edges of the gills and accumulated in the food grooves with some mucus. As can be seen in Figure 10, the food grooves result from an infolding of the frontal surface of the gill filaments. In them the frontal cilia are functionally modified and beat anteriorly, so that the food material passes anteriorly along the ventral edges of the gills to between the labial palps. Here again, sorting is carried out on a size basis (Figure 11).

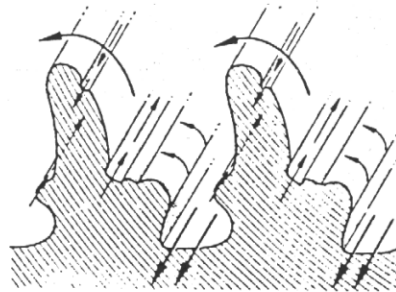
33. Fine material is carried by cilia into the mouth and into the esophagus and stomach, where it undergoes further sorting. Coarser particles accumulate at the edges of the palps and are periodically thrown off by muscular twitches onto the mantle wall. This material, which has been filtered off by the feeding structures but has never entered the gut, is usually called pseudofeces; it is collected by the cleansing cilia of the inside of the mantle wall into ciliary vortices whose arrangement varies in different bivalves. In almost all species the pseudofeces are finally expelled from the bivalve by spasmodic contractions of the adductor muscles which force water, together with the accumulated pseudofeces, out through the normally inhalant openings to the mantle-cavity. All bivalves including unionids show these "spontaneous" spasmodic contractions of the adductor muscles, which thus have a cleansing function. It should be mentioned at this point that the anus and the renal and genital openings are in the exhalant part of the mantle cavity in bivalves, as in all molluscs, and thus expulsion of the wastes or reproductive products is not accomplished by these spasmodic cleansing movements, but by the normal and continuous water flow of the feeding current.

34. Two points should be noted in the diagram of the horizontal section through a half-gill (Figure 11). An additional group of cilia, the laterofrontals, have arisen and serve as a part of the filtering mechanism. In a classic series of research reports, Daphne Atkins (1936; 1937a, b; 1938, 1943) reported beautiful studies by light microscopy on the variation of laterofrontal cilia and on the ciliary mechanisms of various lamellibranch groups. More recently, use of the scanning electron microscope has shown the laterofrontals to be compound cilia, with a finely pinnate structure which greatly increases their efficiency in the trapping of food particles and flicking them onto the frontal collecting tracts (Figure 12). On the other hand, the exhalant sides of the filaments do not have rows of abfrontal cilia





a. On a simple sorting surface, large particles are carried across the ridges, fine particles along the grooves



b. On more complex sorting surfaces, five categories of particles can be sorted in different directions

Figure 11. Ciliated sorting surfaces, which are used externally and internally in molluscs for the mechanical separation of particles of different sizes (from Russell-Hunter 1979)

such as are found on the ctenidia of all other kinds of molluscs. Functionally, this implies that there is no material which penetrates to the exhalant part of the mantle cavity and has to be cleansed off the gill surfaces.

35. A further point is that in such forms as *Mytilus* and *Dreissena*, the adjacent filaments are held together only by occasional ciliary junctions, which function rather like modern dress fastenings of Velcro. In certain other bivalves, such as the unionids, these ciliary junctions are replaced in adults by tissue fusion between adjacent filaments. This character of the nature of the interfilamentary junctions was formerly used in the classification of the bivalves. Recently, however, it has been realized that tissue fusion has been evolved independently in several lines of clams.

36. Incidentally, there is evidence of a totally different sort that the significance of the vast size of the lamellibranch gill is alimentary and not respiratory. If measurements are made of the oxygen consumption of clams, it can be calculated that at the oxygen tensions of their environment, gills of approximately one-fiftieth of the surface area of those developed would suffice for the entire respiratory exchange of such clams.

37. From time to time, claims have been made that mucous sheets are important in the filtration by the gills of lamellibranchs. These have all proved to be wrong, based either on misinterpretation of data on clearance

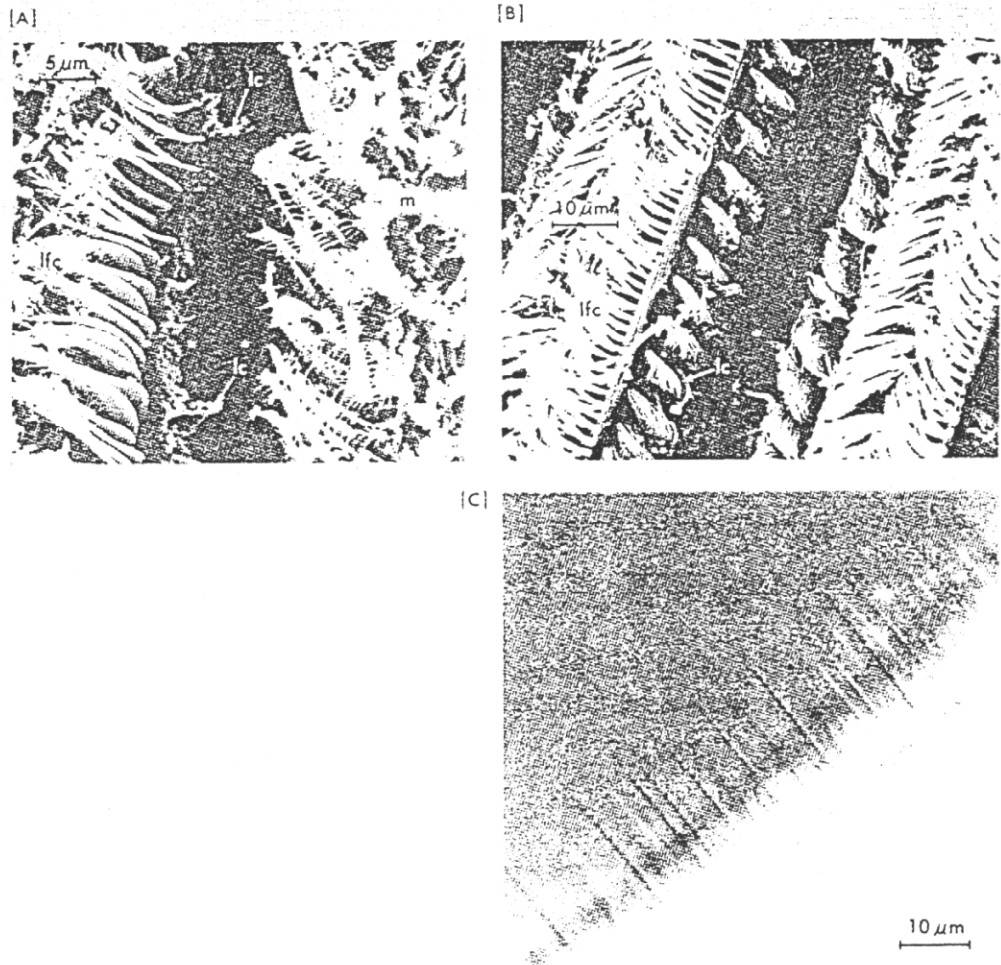


Figure 12. Bivalve laterofrontal cilia as cirri. The great efficiency of the lamellibranch gill as a filter-feeding mechanism depends upon the "additional" group of cilia (the laterofrontals) on each ctenidial filament (see Figure 10 for orientation). A and B: Scanning electron micrographs of adjacent pairs of ctenidial filaments in fact view. C: Interference photomicrograph of the edge of a living gill filament (all from the mussel *Mytilus*). In all photographs the finely pinnate nature of these laterofrontals as compound cilia (or cirri) can be seen. On the right-hand filament in A, the partially extended laterofrontals have been fixed as they cleansed from a small mass of mucus; while both filaments in B (a preparation which had been stimulated with serotonin or 5-hydroxytryptamine, at a concentration which is known to increase water flow through the gill while decreasing particle retention) have the laterofrontals (lfc) folded inward over the frontal cilia, thus "opening" the spaces between the filaments and increasing the efficiency of water propulsion by the lateral cilia (lc), which are seen to be organized in metachronal waves. In the living condition (C) the laterofrontals are shown extended and beating in metachronal rhythm, and thus this photomicrograph constitutes a "food-particle's-eye" view of the filtering apparatus of a typical lamellibranch bivalve. (From Russell-Hunter 1979, photos courtesy of Dr. C. Barker Jorgensen of the University of Copenhagen).